

Distribution and richness of amphibians under different climate change scenarios in a subtropical region of South America

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ABSTRACT

Amphibians are a valuable indicator group to study potential impacts of climate change (CC) because reproduction is closely linked to the availability of freshwater. Climate projections for the humid subtropical region of South America predict an increase in temperature towards the southwest and an increasing of precipitation during the rainy season and decreasing during the dry season. In this context, we aimed to predict the changes in the distribution range of amphibian species and the variation in their richness. In addition, we attempted to determine the most vulnerable species in terms of the extent of habitat loss and the overlap of optimal species distributions by contrasting present and future species range. We modelled the current and future distribution of 55 amphibian species using an inductive approach to model the ecological niche with three different algorithms. We used WorldClim data for current climate and IPCC5 climate projections from Global Climate Model for two greenhouse gas concentrations at 2050. Depending on the CC scenario, between 48 and 57% of the species showed a decrease in their optimal distribution, and 9–10% of them are likely to be affected by further population fragmentation. We identified three types of patterns of change in the geographical distribution of the optimal areas: (I) reduction, (II) displacement, and (III) increase in their distribution range. Future new areas with favourable conditions may not be reached due to the low dispersion tendency of amphibians. For this reason, it is important to identify those current favourable areas that are maintained in the different future scenarios. In this sense, this study allows to highlight priority areas for the conservation of the studied species and to identify those being highly vulnerable to the predicted scenarios. Our results contribute to the knowledge of how different future climates scenarios could affect the conservation of the studied amphibian species and provide key information for the development of strategies and public policies for management and biodiversity conservation.

1. Introduction

Climate is the major determinant of the distribution of terrestrial organisms and richness patterns at large scales (e.g., Currie, 2001; Guisan & Thuiller, 2005; Nix, 1982, p. 47). Projections of future climate conditions predict that major changes will take place in most subtropical regions globally, including an increase in average global temperature, a decrease in precipitation and changes in their annual patterns (Allison et al., 2009; Brinson, 2006, pp. 25–33; Christensen et al., 2007, chap. 11; IPCC, 2008; Zank et al., 2014). As a result, species are expected to modify their geographic range (Hughes, 2000; Parmesan, 2006; Parmesan & Yohe, 2003).

Over the last decades, several studies have analysed how particular

species, communities and habitats react to climate changes (e.g., Benito Garzón, Sánchez de Dios, & Sainz Ollero, 2008; Cianfrani, Broennimann, Loy, & Guisan, 2018; Loehle & LeBlanc, 1996; Walther et al., 2002). In recent years, the understanding of species range shifts in response to changing environmental processes has gained recognition (Austin, 2002; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000) as it provides valuable information to design species conservation strategies (Falcucci, Maiorano, & Boitani, 2007; Rustigian, Santelmann, & Schumaker, 2003) like selection of priority conservation areas (Kuemmerle et al., 2011; Margules, Pressey, & Williams, 2002). This approach has been used in relation to land-use/land-cover change and landscape transformation under different development scenarios (White et al., 1997) to examine a possible link between ongoing climate

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change and species declines (e.g., Araujo & Guisan, 2006; Benito Garzón et al., 2008).

The geographical distribution of the species and further variations due to changes in environmental conditions can be analysed using niche models, which are based on species-environment relationships (Guisan & Zimmermann, 2000) and developed from a set of algorithms (de Souza Muñoz et al., 2011). Niche modelling has been used to predict species ranges, by combining geographical points with presence, absence and/or abundance data, together with environmental variables under past, present or future scenarios (Araújo & Peterson, 2012; Beaumont, Hughes, & Poulsen, 2005; IPCC, 2008). Recently, numerous studies have used niche modelling to investigate the impacts of climate change on species distribution (Guisan & Thuiller, 2005; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Anderson, 2013; Bradie and Leung, 2017).

The predictions of the Intergovernmental Panel on Climate Change (IPCC, 2008) regarding the consequences of global climate change in South America are still rather imprecise and somewhat contradictory (Junk, 2013). However, rainfall distribution during annual cycles may change, with precipitation increasing during the rainy season (summer) and decreasing during the dry season (winter) (Vera, Silvestri, Liebmann, & González, 2006; Nuñez, Solman, & Cabré, 2009). Also, an increase of extreme multiannual and short-term climate events (El Niño and La Niña, heavy rains and droughts, heat waves) is predicted (Nuñez et al., 2009). Climate model HadGEM2-ES performed by Met Office Hadley Centre (United Kingdom) and Instituto Nacional de Pesquisas Espaciais (Brazil) show scenarios of increased rainfall in South America southeast and a decrease at summer in flooded grasslands and savannas at southwest of Brazil (spatial dataset available at http://www.worldclim.org/CMIP5_2.5m). In northern and central Argentina especially, increase in precipitation in summer and fall and a general decrease in precipitation in winter and spring is projected (Nuñez et al., 2009). In addition, it predicts an increase in temperatures towards the southwest of La Plata Basin (LPB), for both scenario of lower and higher emission of radiative forcing (IPCC, 2014). The impact of the rise in temperature on the species composition of South American wetlands is difficult to predict, given the lack of ecophysiological data on wetland organisms (Junk, 2013).

A particular focus has been placed on amphibians because of their close dependence on temperature, precipitation and hydrological regimes (Cayuela, Besnard, Bechet, Devictor, & Olivier, 2012; Jakob, Poizat, Veith, Seitz, & Crivelli, 2003; Ortiz-Yustá, Páez, & Zapata, 2013; Rustigian, Santelmann, & Schumaker, 2007, pp. 108–114) and because their populations are declining globally (Alford & Richards, 1999; Reading, 2007). On one hand, they are ectotherms: their patterns of activity, hibernation, reproductive phenology and calling and breeding behavior are conditioned by temperature (Lluisa et al., 2013). On the other, many species begin their reproductive season with rains. Its reproductive success is closely linked to the quality and availability of water bodies where they mate, deposit their eggs and develop into larvae (Ojima & Lockett, 2000; Walls, Barichivich, & Brown, 2013; Wells, 2010, p. 1400). At present, 1856 (32.5%) amphibian species are considered as threatened (IUCN, 2015). This situation results from multiple causes including habitat loss and degradation (Blaustein & Wake, 1990; GAA, 2006; Gagné & Fahrig, 2007; Stebbins & Cohen, 1995) and will become even worse by draughts, as predicted by future climate scenarios (Walls et al., 2013). Wetlands, which are the most affected ecosystems by climate change worldwide (Desta, Lemma, & Fetene, 2012), provide amphibians with habitat requirements to complete their life-cycle. Consequently, they respond rapidly to changes in the environmental conditions of these ecosystems (Hopkins, 2007).

In this paper, we aimed to predict the changes in the distribution range of 55 amphibian species under two potential future climate scenarios for the subtropical region of southern South America. In addition, we attempted to determine the most vulnerable species in terms of the extent of loss and overlap of optimal species habitats by contrasting present and future distributions. We expect that 1) most species will retract their distributions in response to the expected temperature

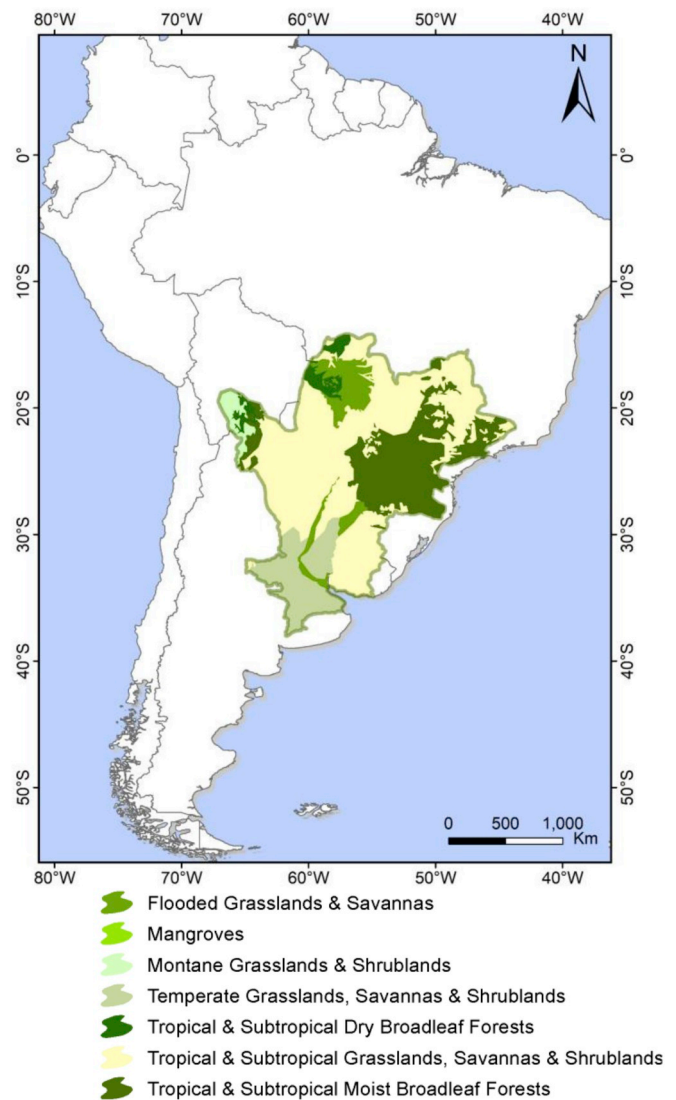


Fig. 1. Map of South America showing main LPB biomes, the selected area for a more detailed analysis of potential changes in the distribution of the studied amphibian species.

increase and their limited ability to disperse into new favourable areas, and 2) tropical and subtropical species will find favourable conditions to the southeast by increased rainfall.

2. Methods

2.1. Study area

We considered the whole subcontinent of South America for modelling the potential distribution of the studied amphibian species in order to include the natural variability in their current geographical ranges (Fig. 1). In that subcontinent, a detailed analysis was made in the subtropical-temperate region of La Plata Basin (LPB), which includes the north-eastern part of Argentina as well as the south-eastern Brazil, the southern Paraguay and Uruguay (Fig. 1, green area).

The main biomes or major habitat types represented in LPB are Tropical & Subtropical Grasslands Savannas & Shrublands (53.6%), Tropical & Subtropical Moist Broadleaf Forests (22.6%), Temperate Grasslands, Savannas & Shrublands (10.8%), Flooded Grasslands & Savannas (7.3%), Tropical & Subtropical Dry Broadleaf Forests (3.2%), Montane Grasslands & Shrublands (2.4%) and Mangroves (0.002%) (Olson et al., 2001). Most of this habitats are threatened by cattle

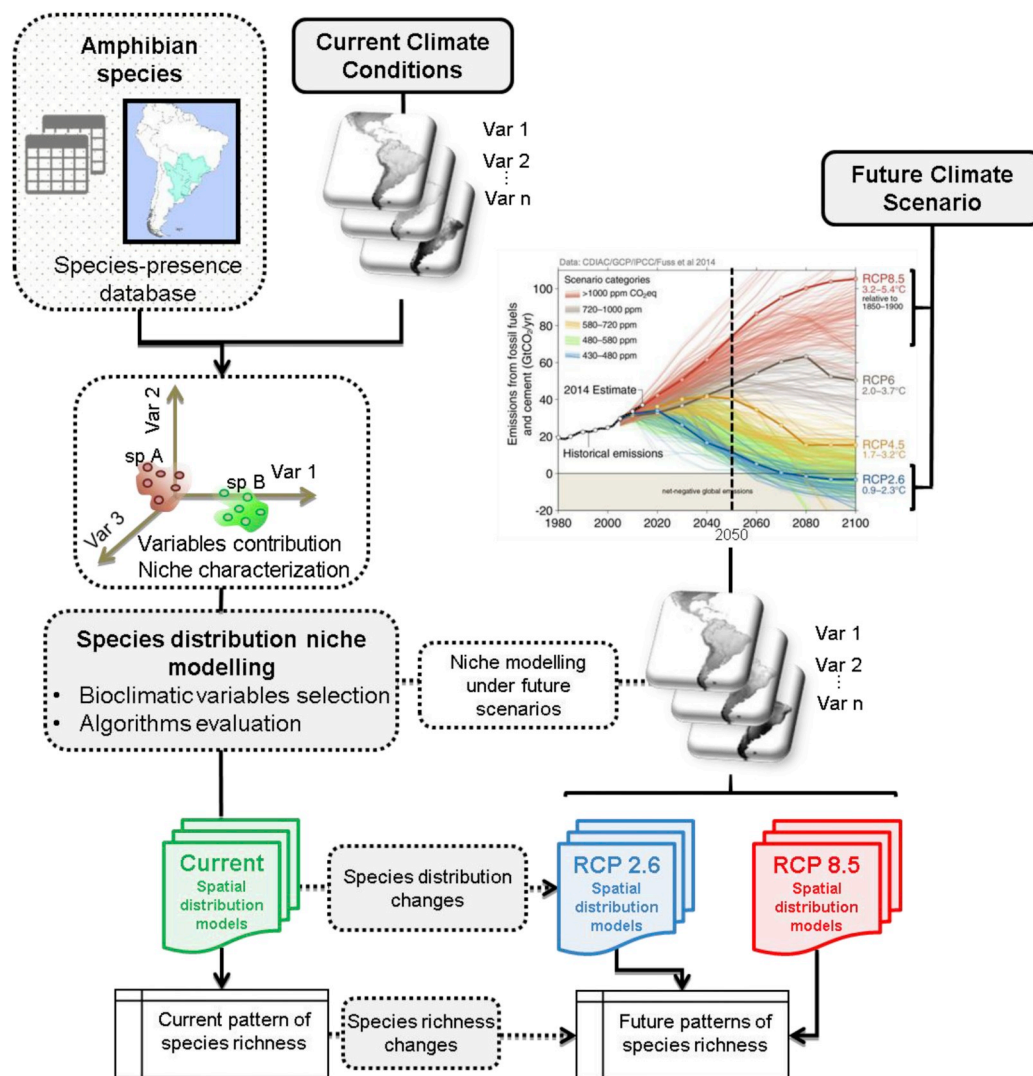


Fig. 2. Methodological diagram for modelling the amphibians' distribution and richness using niche models under current and future climate scenarios.

grazing, agricultural expansion and afforestation (Baldi, Guerschman, & Paruelo, 2006).

Several authors have predicted that this region will experience increasing trends in temperature (1–5 °C) and rainfall (0.5–1 mm day⁻¹), mainly an increase in summer rainfall in the subtropical south-east (Nuñez et al., 2005, 2009; Solman, Nunez, & Cabré, 2008) by the end of this century, with potential impacts on the regulation of the breeding season in amphibians (Donnelly & Crump, 1998, pp. 401–421).

2.2. Occurrence databases and distribution models of species

We developed distribution models for 55 amphibian species using different algorithms based on statistical functions that describe relationships between species occurrences and corresponding environmental variables (Guisan & Zimmermann, 2000, Fig. 2).

Amphibian species were characterized according to the period, type and breeding site, and habitat specificity from bibliographic data (Prado, Auetanabaro, & Haddad, 2005). They were grouped into ecological groups by cluster analysis with Gower distance matrices because the binary nature of the variables and average linkage (Di Rienzo et al., 2011, pp. 195–199).

For species-presence data, georeferenced records of the studied amphibian species in the study area (Vaira et al., 2012; Zaracho, Céspedes, Álvarez, & Lavilla, 2012, Appendix A) were obtained from the Global Biodiversity Information Facility -GBIF- database (Anderson

et al., 2016). Complementary, bibliographic records were digitised and incorporated into the analysis (Ingaramo et al., 2012; Narvaes & Rodrigues, 2009; Zank et al., 2014). All duplicate and incomplete georeferenced data were removed. Pseudo-absence records to evaluate the obtained model were generated according to VanDerWal, Shoo, Graham, and Williams (2009) and Barbet-Massin, Jiguet, Albert, and Thuiller (2012). The number of pseudo-absences was equal to the number of presences for each species within the area occupied.

Environmental variables, which were used to characterise the niche and to model the potential distribution of each species, were taken from the current bioclimatic conditions calculated by interpolations of observed data, representative of 1960–1990, provided by WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These variables are expressed as indices calculated from monthly precipitation and temperature records from weather stations located around the world (more details see O'Donnell & Ignizio, 2012). The index values allow to identify the environmental conditions in which species may occur. The fact that some bioclimatic variables are obtained from the same measurements may lead to redundancy between predictors (Table 1). For this reason, ecological niche models based on the full set of variables can increase over-fitting of the model, especially for species with few occurrence data (Beaumont et al., 2005). Therefore, we applied a correlation analysis to avoid collinearity of bioclimatic variables (Dormann, Puschke, Márquez, Lautenbach, & Schröder, 2008; Guisan & Thuiller, 2005; Phillips & Elith, 2010). Although hydrology is a key

Table 1

Bioclimatic variables derived from monthly precipitation and temperature data with a spatial resolution of 2.5 min (Source: WorldClim – Global Climate Data, Available at: [<http://www.worldclim.org/>]. Further information and variables details see O'Donnell & Ignizio, 2012, Available at: [<https://pubs.usgs.gov/ds/691/ds691.pdf>]). *Non-correlated variables were used for the generation of species distribution models.

Variable	Code	Description
Temperature	BIO1 *	Annual Mean Temperature
	BIO2 *	Annual Mean Diurnal Range (Diurnal _{monthly} range = (max _{monthly} temp - min _{monthly} temp))
	BIO3	Isothermality (BIO2/BIO7) (*100)
	BIO4	Temperature Seasonality (standard deviation *100)
	BIO5 *	Max Temperature of Warmest Month
	BIO6	Min Temperature of Coldest Month
	BIO7	Temperature Annual Range (BIO5-BIO6)
	BIO10	Mean Temperature of Warmest Quarter
	BIO11	Mean Temperature of Coldest Quarter
	BIO12 *	Annual Precipitation
	BIO13	Precipitation of Wettest Month
Precipitation	BIO14 *	Precipitation of Driest Month
	BIO15	Precipitation Seasonality (Coefficient of Variation)
	BIO16	Precipitation of Wettest Quarter
	BIO17	Precipitation of Driest Quarter
Temperature and Precipitation	BIO8	Mean Temperature of Wettest Quarter
	BIO9	Mean Temperature of Driest Quarter
	BIO18 *	Precipitation of Warmest Quarter
	BIO19	Precipitation of Coldest Quarter

factor, it is difficult to model at long term and large scale because is influenced by other factors like land use-land cover changes (Collischonn, Tucci, & Clarke, 2001). On the other hand, precipitation has been the major cause of increases in river flows within the Paraná basin since 1970 (Tucci & Clarke, 1998). In particular, for the study region, precipitation accounts for 53–85% of the variation in the hydrometric level of the Paraná basin (Maheu, Cazenave, & Mechoso, 2003). Therefore, in this work, we considered variables associated to precipitation as an indicator of hydrology regimen of this basin. Hence, the variables used to characterise and model current and future distributions were restricted to the set of bioclimatic variables derived from monthly precipitation and temperature.

We used three different algorithms for generating predictive species distribution models: 1) BIOCLIM, which determines the potential distribution of a species from profile analysis or bioclimatic envelopes (Busby, 1991; Farber & Kadmon, 2003; Fischer, Lindenmayer, Nix, Stein, & Stein, 2001; Lindenmayer, Nix, McMahon, Hutchinson, & Tanton, 1991; Nix & Busby, 1986); and 2) DOMAIN, which calculates the similarity between each occurrence point of a species and every other point of the space through the Gower distance (Carpenter, Gillison, & Winter, 1993; Hijmans, Guarino, & Mathur, 2004) and 3) MaxEnt, which is a machine-learning technique which estimate a probability of presence, cloglog output, to predict distribution (Merow, Smith, & Silander, 2013; Phillips, 2017; Phillips, Anderson, & Schapire, 2006).

These modelling approaches assume that: 1) species cannot adapt to climatic conditions different from those existing today, 2) bioclimatic variables are the main drivers of species geographic distribution and 3) species dispersal is unlimited (Guisan & Zimmermann, 2000). BIOCLIM and DOMAIN algorithms were implemented in DIVA-GIS 7.5 software for mapping and analysis of geographic data (available at <http://www.diva-gis.org/>). MaxEnt algorithm were executed in an open-source software programed in Java language (available at https://biodiversityinformatics.amnh.org/open_source/maxent/). We used 75% of the presence records to obtain the models and reserved the remaining 25% for evaluating the performance of the algorithms. This process was repeated ten times, each time one distribution model was generated. For replication bootstrap method was applicate, where the

training data is selected by sampling with replacement (Phillips et al., 2006). The importance and contribution of each bioclimatic variable to the distribution model for each species was evaluated in a particular and global way through the jackknife test. This procedure allowed to identify the importance of each of the six bioclimatic variables in the generation of each distribution model for each species.

2.3. Evaluation of algorithms

For the evaluation of the models' performance, the mentioned subset of data reserved for this purpose were used. The best algorithm to model the current species distribution was selected by evaluating the predictive power of each one. In this sense, we used the sensitivity and specificity in a binary classifier and calculate the area under the curve ROC (AUC) (Elith & Burgman, 2002, pp. 303–314; Hijmans et al., 2004; Fawcett, 2006; Morán-Ordóñez et al. 2017).

2.4. Future scenarios

The uncertainty of how climate will change points to the importance of using multiple climate change scenarios (Watling, Brandt, Mazzotti, & Románach, 2013). In this context, we considered two different representative concentration pathways (RCPs) scenarios of concentration of greenhouse gases (GHGs) for 2050 (IPCC, 2014): +2.6 and +8.5 W/m² (hereafter referred to as 26_50 and 85_50, respectively). These represent the two extreme scenarios of concentration of GHGs obtained from the last model proposed by the IPCC Fifth Assessment (IPCC, 2014): the HadGEM2-ES (Met Office Hadley Centre, United Kingdom and Instituto Nacional de Pesquisas Espaciais, Brazil), which have the same spatial resolution as those provided by the WorldClim database (2.5 min) and are available at http://www.worldclim.org/CMIP5_2.5m.

2.5. Shifting patterns of species distribution and richness

For each species, we estimated the size and number of suitable patches at the core of present and future distribution areas as well as their overlapping areas. Core area is defined as the area with the highest probability of species occurrence. In addition, patterns of amphibian richness were analysed for both periods by overlapping the distribution of each species (Currie, 2001; White et al., 1997).

We assessed changes in species richness by comparing values of the IndCoR index between periods. This index, conceived as the ratio between current and future species richness, is used to generate a layer representing the risk of species richness loss (Meynecke, 2004). IndCoR ranges between 0 and +∞; values close to 1 indicate that species richness remains unchanged, values close to 0 indicate higher predicted species richness, and values greater than 1 indicate lower predicted species richness. We identified the amphibian species most vulnerable to climate changes according to recent distribution changes and current conservation status (IUCN, 2015; Sekercioglu, Schneider, Fay, & Loarie, 2008).

3. Results

For the 55 amphibian species considered in the study area we obtained 5760 georeferenced occurrence records. For seven species (*Argenteohyla siemersi*, *Leptodactylus diptyx*, *Melanophryniscus atroluteus*, *M. devicenzi*, *M. klappenbachii*, *Pseudis platensis* and *R. ornata*), they did not have enough records to model their distribution.

From the ecological traits, 6 groups were obtained (Appendix B):

- **G1** (10 species) characterized by reproduction during spring-summer whose reproductive type is unknown in temporary environments.
- **G2** (9 species) with prolonged annual reproduction in vegetation associated with water bodies.
- **G3** (10 species) with continuous spring-summer reproduction type

in temporary environments.

- **G4** (11 species) with spring-summer reproduction of explosive type after heavy rains.
- **G5** (*Hypsiboas pulchellus*) characterized mainly by having reproduction in autumn-winter.
- **G6** (*Lepidobatrachus asper*) characterized by explosive reproduction after rains in Xerophytic Forest.

Of the three algorithms used, the best AUC values were obtained with MaxEnt (Appendix C). With this algorithm, the geographical distributions of 48 species were obtained (See Figures E. 01 to E. 48 in Appendix E). Of these species, six (*Hypsiboas caingua*, *H. punctatus*, *Leptodactylus fuscus*, *Physalaemus riograndensis*, *Pseudopaludicola boliviana* and *Siphonops paulensis*) have enough number of occurrence records to generate the distribution models but the results only indicated the presence of areas of low probability within the study area (Appendices C and E).

Of the six selected bioclimatic variables excluding collinearity, three contributed to 74.4% of the MaxEnt model: BIO01 average annual temperature (28.7%), BIO18 precipitation of the warmest quarter (25.3%) and BIO12 annual precipitation (20.4%) (Fig. 3 and Appendix D).

The species whose distribution responds to BIO01 and BIO18 are, in general, species that have annual reproduction. While those species with reproduction after heavy rains associated with temporary waterbodies respond to BIO12 and BIO18. (Appendices B and D). Particular cases as *Hypsiboas pulchellus* whose distribution is mainly associated with BIO01 may be due it does not necessarily depend on waterbodies

for its reproduction and its reproductive peak is in autumn-winter (G5, Table 2).

Most of the studied species showed a potential decrease in their optimal distribution areas: 23 (54.8%) and 20 (47.6%) of the species in both the 26_50 and the 85_50 scenarios, respectively. While in both scenarios 4 species (9.5%) did not show substantial changes (Tables 2 and 3). In addition, the potential distribution range of 9 (21.4%) and 7 (16.7%) species shows a highly fragmented distribution (an increase in patch number) under the 26_50 and 85_50 scenarios, respectively (Table 3). In particular, *Phyllomedusa sauvagii* and *Trachycephalus typhonius* exhibited a decrease in size in their optimal distribution ranges as well as a greater fragmentation of them (Tables 3 and 4).

Furthermore, the comparison of the current and future distribution ranges of species and the overlapping between them (Table 4) resulted in three types of generalized patterns: I) Net decrease in the potential distribution range. Current area is lost and new areas are not generated, this is reflected in a negative difference between the current and future area (e.g., *Leptodactylus gracilis*, Fig. 4 Type I); II) Shift in the distribution range. Little overlap between current and future distributions because of generation of new areas and loss of original ones. In this type, those species that presented little or no overlap were included (e.g., *Scinax acuminatus*, Fig. 4 Type II); and III) Conservation of more than 40% of the current distribution and the incorporation of new optimal areas which results in a net increase of its distribution range, this is reflected in a positive difference between the current and future area (e.g., *Rhinella bergi*; Fig. 4 Type III).

Type I pattern was the most frequent with 18 species (43%). Type II

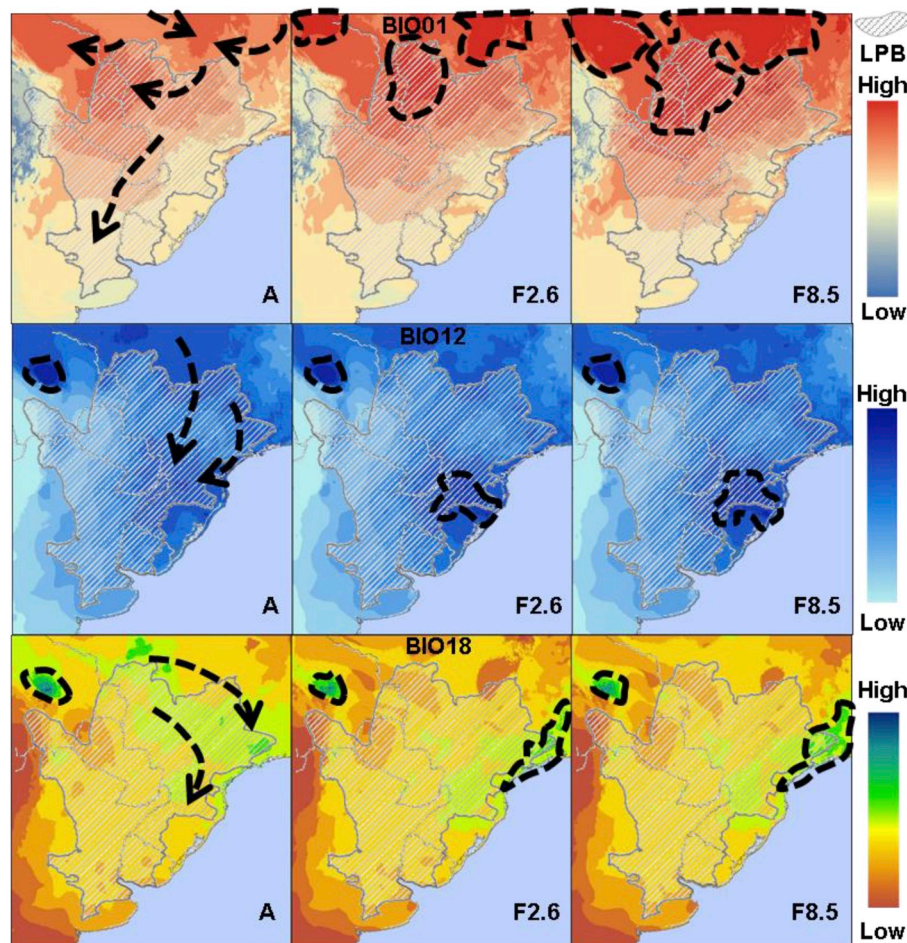


Fig. 3. Bioclimatic variables with the highest contribution to the modelling of distribution range of the studied amphibian species. BIO01: Annual Mean Temperature, BIO12: Annual Precipitation and BIO18: Precipitation of Warmest Quarter (A: bioclimatic current conditions, F2.6: +2.6 W/m², and F8.5: +8.5 W/m²). Dotted lines delimit the areas where the bioclimatic variable has high values. The arrows indicate the direction of change of the isolines for each variable.

Table 2Percentage contribution of the bioclimatic variables for each ecological group (mean \pm standard error).

Ecological group	Species	BIO01	BIO02	BIO05	BIO12	BIO14	BIO18
		Mean (+/- SE)	Mean (+/- SE)	Mean (+/- SE)	Mean (+/- SE)	Mean (+/- SE)	Mean (+/- SE)
1	10	29.7 (4.6)	6.1 (1.7)	1.3 (0.4)	21.1 (6.4)	15.8 (4.9)	25.9 (5.8)
2	9	26.4 (2.6)	9.6 (0.8)	2.2 (0.5)	16.0 (2.9)	13.0 (3.4)	32.8 (4.7)
3	10	23.3 (3.3)	8.4 (1.2)	1.0 (0.3)	17.9 (4.5)	17.0 (5.8)	32.3 (5.0)
4	11	33.6 (7.0)	6.9 (1.9)	1.4 (0.3)	22.6 (5.3)	15.8 (3.5)	19.6 (4.9)
5	1	47.9	3.8	3.7	3.9	7.4	33.3
6	1	45.7	1.4	0.3	22.2	3.4	27.1

Table 3Number of species showing potential changes in their distribution range and in the number of patches resulting from habitat fragmentation under the two considered GHG climate forcing scenarios: Representative Concentration Pathways +2.6 (RCP 2.6) and +8.5 W/m² (RCP 8.5).

		RCP 2.6		RCP 8.5	
		Patch number		Patch number	
		Increase	Decrease	Increase	Decrease
Distribution range	Increase	5 (12%)	10 (24%)	4 (10%)	14 (33%)
	Equal	2 (5%)	2 (5%)	1 (2%)	3 (7%)
	Decrease	2 (5%)	21 (50%)	2 (5%)	18 (43%)

and III presented both 11 species (26%), whereas the remaining two species (5%) exhibited a pattern which could not be associated with any of the identified types (Table 4 and Appendix E).

An average overlap of 24% was observed when comparing the current distribution areas and those defined in the two future scenarios (Table 4). The species from G3 and G5 resulted in the smallest area of optimal distribution preserved in future scenarios. While *Lepidobatrachus asper* (G6) was the group with largest overlap area presented. In particular, 6 species in each scenario (*Trachycephalus typhonius* and *Leptodactylus bufonius* in both) did not show overlap area of their future optimal distribution respect to current conditions (Tables 4 and 5).

Fig. 5 shows the richness of the considered amphibian species under current and potential future climate scenarios. Overall, for the studied area, our models predict that species richness will increase south and northeastward and will decrease northward.

Finally, the IndCoR figure summarizes the temporal variation of species richness. In red the areas with a greater richness of amphibian species in the current conditions while in green the areas with a greater future richness. Similar IndCoR geographic pattern was found for both future projected scenarios (Fig. 6).

4. Discussion

We studied the potential impacts of climate change on the distribution of amphibian species in a subtropical-temperate region of South America. Taking into account the little information available on this issue for South American amphibians and the accelerated decline of so many species, our results are helpful to develop appropriate conservation policies in this region.

Despite the wide use of BIOCLIM and DOMAIN algorithms to analyze the biogeographic distribution of numerous species (e.g., Booth, Nix, Busby, & Hutchinson, 2014; Naoki, Gómez, López, Meneses, & Vargas, 2006; Nix & Busby, 1986), in our work we obtained better results with MaxEnt algorithm in agreement with other authors (Hernandez, Graham, Master, & Albert, 2006; Hijmans & Graham, 2006). It should be noted that MaxEnt has shown a better performance in comparison with other algorithms (Elith et al., 2006; Preau, Trochet, Bertrand, & Isselin-Nondedeu, 2018), in particular when there are few points of presence (Morales, 2012). The model using BIOCLIM is based

on traits obtained from extreme values. The fact that each bioclimatic variable is treated independently may lead to unrealistic variable combinations, weak ecological predictions and overestimated distributions (Carpenter et al., 1993). An important advantage of DOMAIN over BIOCLIM is that it uses a similarity measure rather than the extreme traits of the species climate envelope to predict distribution changes (Carpenter et al., 1993; Naoki et al., 2006) but tend to underestimate species ranges (Hijmans & Graham, 2006).

The species distribution models are scale-dependent according to the nature of the predictor variables (Guisan & Zimmermann, 2000; Manzoor, Griffiths, & Lukac, 2018). Our models aim to predict regional distribution patterns (large scale); however it is necessary to consider that at local level there may be other variables operating that explain the presence or absence of a species in a certain site. Large-scale patterns of species distribution and richness are not only determined by environmental features but also by evolutionary history (Gaston, 2000; Wiens & Donoghue, 2004). Some species have specific habitat requirements (e.g., availability of permanent water bodies) or are affected by local characteristics (e.g., distance to urban centres). As an example, species like *Leptodactylus mystacinus*, *Dermatonotus muelleri* and *Phyllomedusa sauvagii* besides decreasing their future distribution they may be affected locally because their bioclimatic optimal area can change to sites that do not have specific land cover habitat requirement. In this sense, differences between observed and expected distributions may result from local phenomena not related to general climatic conditions. To solve these discrepancies, it has been recommended to use the same algorithm with other variables that account local phenomena or processes (Larson, Degroot, Bartholomay, & Sugumaran, 2010). For that reason, this type of variables, different from bioclimatic ones, could be used in order to generate local distribution models with a higher spatial resolution. On the other hand, amphibians usually have a low dispersal capacity as they are highly phylopatric, meaning that they tend to remain close to their natal area (e.g. Smith & Green, 2005; Blaustein, Wake, & Sousa, 1994; Sinsch, 1991). Furthermore, some authors advise to consider the hypothesis of non-dispersal for this group (e.g., Araújo, Thuiller, & Pearson, 2006). Therefore, their distributions are expected to be restricted to areas where their present and potential future ranges overlap. In both future climate forcing scenarios the predicted distribution areas represent less than 25% of the present-day distributions for more than 60% of the studied amphibian's species. In the worst scenario, species with continuous reproduction (*sensu* Crump, 1974) had a low percentage of overlap between their current habitat and the future one while species that depend on rainfall had a higher percentage of overlap. This may be related to the fact that in LPB a higher increase in annual rainfall is projected in the worst scenario, causing a higher level of overlap for species that depend on rain for reproduction. *Lepidobatrachus asper* is a clear example of this situation since it has the most-depend life cycle on rainfall and showed the highest percentage of overlap for both scenarios. Similarly, an extreme increase in temperature is projected for the worst scenario, which could affect those species whose distribution responds to annual average temperature range or annual temperature, as is the case of amphibians that breed throughout the year. However, it is important to stand out that in all cases there is a decrease in the percentage of

Table 4

Characteristics of both the optimal distribution area of each species obtained with MaxEnt for current climatic conditions (WorldClim v1.4) and the overlapping areas between present and potential future distribution areas and their difference (future – current). Potential scenarios to 2050 were obtained with the HadGEM2-ES model for GHG climate forcing at concentrations of +2.6 W/m² (26_50) and +8.5 W/m² (85_50). The area of patches is expressed in 10³ Km². PN: patch number. See Appendix B for acronyms of species names.

Acronym	Current	26_50												85_50												Type	Ecological group
		Future				Overlap				Difference				Future				Overlap				Difference					
		10 ³ Km ²	PN	10 ³ Km ²	PN	10 ³ Km ²	%	PN	10 ³ Km ²	%	PN	10 ³ Km ²	PN	10 ³ Km ²	%	PN	10 ³ Km ²	%	PN								
<i>Rhin_ber</i>	767	85	835	109	550	72	80	68	9	24	986	74	583	76	66	218	28	−11	III	1							
<i>Rhin_ict</i>	50	79	37	46	11	23	50	−13	−26	−33	26	31	16	33	37	−23	−47	−48	I	1							
<i>Pseu_min</i>	16	26	10	3	6	38	6	−6	−35	−23	9	5	4	23	8	−7	−46	−21	I	1							
<i>Scin_fuv</i>	90	80	46	40	17	19	27	−44	−49	−40	51	44	7	8	26	−39	−44	−36	I	1							
<i>Scin_sim</i>	0	5	0	5	0	0	5	0	33	0	0	3	0	100	5	0	56	−2	Unclass	1							
<i>Lept_buf</i>	132	28	6	12	0	0	2	−127	−96	−16	3	14	0	0	0	−130	−98	−14	I	1							
<i>Lept_lab</i>	359	140	243	79	112	31	85	−116	−32	−61	127	51	34	9	44	−232	−65	−89	I	1							
<i>Phys_bil</i>	149	45	49	31	37	25	17	−100	−67	−14	71	32	41	28	16	−78	−52	−13	I	1							
<i>Derm_mue</i>	134	49	162	42	56	42	14	28	21	−7	150	19	20	15	10	16	12	−30	III	1							
<i>Chth_ind</i>	153	77	29	10	25	17	13	−124	−81	−67	44	13	39	25	11	−109	−71	−64	I	1							
<i>Scin_acu</i>	102	52	238	63	57	56	25	136	134	11	320	32	31	30	34	218	214	−20	III	2							
<i>Scin_nas</i>	73	80	85	20	29	40	26	11	16	−60	155	17	25	34	20	82	113	−63	III	2							
<i>Scin_squ</i>	37	90	19	6	6	16	14	−18	−48	−84	21	15	6	16	13	−16	−44	−75	I	2							
<i>Lept_pod</i>	75	73	161	12	53	70	25	86	115	−61	225	9	49	65	26	150	200	−64	III	2							
<i>Pseu_mys</i>	185	114	214	74	0	0	0	30	16	−40	155	56	4	2	6	−30	−16	−58	II	2							
<i>Phys_alb</i>	51	46	107	15	17	33	11	56	110	−31	209	16	0	0	0	158	308	−30	II	2							
<i>Odon_ame</i>	89	111	24	5	18	20	3	−65	−73	−106	17	3	13	14	3	−72	−81	−108	I	2							
<i>Phylsau</i>	136	17	43	21	19	14	12	−93	−68	4	58	21	34	25	14	−78	−57	4	I	2							
<i>Pith_aze</i>	112	41	323	83	48	43	26	211	188	42	460	80	17	15	13	348	310	39	III	2							
<i>Dend_nan</i>	13	51	8	13	1	10	18	−5	−39	−38	49	17	1	10	12	36	279	−34	II	3							
<i>Dend_san</i>	63	35	8	13	2	2	6	−55	−87	−22	64	21	1	1	5	1	1	−14	II	3							
<i>Hyps_alb</i>	128	197	47	88	14	11	25	−80	−63	−109	37	46	4	3	20	−90	−71	−151	I	3							
<i>Hyps_ran</i>	67	57	133	14	35	52	31	66	99	−43	219	8	40	60	28	152	227	−49	III	3							
<i>Scin_ber</i>	27	33	18	8	3	11	3	−10	−35	−25	20	13	3	12	3	−7	−27	−20	I	3							
<i>Scin_fum</i>	182	98	129	43	69	38	27	−52	−29	−55	154	36	59	33	23	−27	−15	−62	I	3							
<i>Lept_ele</i>	81	39	211	25	41	51	16	130	160	−14	377	30	40	49	14	295	363	−9	III	3							
<i>Lept_gra</i>	153	110	8	22	4	2	14	−144	−95	−88	5	8	1	0	6	−148	−97	−102	I	3							
<i>Lept_lat</i>	63	30	38	23	9	14	15	−24	−39	−7	78	7	14	22	13	15	24	−23	II	3							
<i>Lept_mys</i>	26	5	37	7	0	0	0	12	44	2	164	78	2	8	6	138	532	73	II	3							
<i>Rhin_fer</i>	37	55	13	14	15	40	19	−23	−64	−41	45	7	16	45	15	8	23	−48	II	4							
<i>Rhin_gra</i>	46	10	46	2	5	11	9	0	0	−8	53	10	16	36	7	7	15	0	II	4							
<i>Rhin_sch</i>	87	76	95	17	10	11	3	8	10	−59	87	17	0	0	1	0	1	−59	II	4							
<i>Lysa_lim</i>	138	97	178	45	45	33	55	39	29	−52	342	91	76	55	68	203	147	−6	III	4							
<i>Trac_typ</i>	77	25	33	80	0	0	0	−44	−58	55	46	77	0	0	0	−31	−40	52	II	4							
<i>Lept_cha</i>	21	50	59	8	0	1	3	38	181	−42	97	15	0	0	2	77	368	−35	II	4							
<i>Lept_ltr</i>	104	57	39	5	28	27	5	−66	−63	−52	33	2	24	23	2	−72	−69	−55	I	4							
<i>Pseu_fal</i>	110	128	16	12	14	13	11	−94	−85	−116	7	6	6	5	6	−103	−94	−122	I	4							
<i>Phys_cuv</i>	276	66	148	44	124	45	36	−128	−46	−22	120	55	55	20	50	−157	−57	−11	I	4							
<i>Phys_san</i>	0	3	0	4	0	0	3	0	75	1	0	3	0	100	3	0	250	0	Unclass	4							
<i>Elac_bi</i>	205	51	204	28	123	60	12	−1	0	−23	266	36	109	53	10	61	30	−15	III	4							
<i>Hyps.pul</i>	44	39	13	22	10	23	5	−31	−70	−17	11	30	8	17	6	−34	−76	−9	I	5							
<i>Lepi_asp</i>	104	12	306	69	80	77	15	203	196	57	440	53	91	88	13	336	324	41	III	6							

overlap of the areas as a consequence of a future reduction or shift of optimal areas. This may be related to the decrease in precipitation in the warmest quarter projected for LPB in both scenarios, which was the second relevant variable in determining the current distribution of most of the amphibian species in the basin. At the lower GHG concentration a critical reduction of their distribution range was observed for *Leptodactylus bufonius*, *L. mystacinus*, *Pseudopaludicola mystacalis* and *Trachycephalus typhonius*. Consequently, they did not show an overlap between present and potential future distribution areas. Anyway, a more pronounced shrinkage of overlapping areas became evident at the higher GHG concentration. In addition, under both scenarios, six species with change patterns types I and II presented less than 5% overlap. In contrast, future changes would be favourable for the 21% of species, which showed a pattern type III.

Of the three identified patterns of changes in the species' distribution, the few amphibian species that show the incorporation of new areas in their distribution range under future scenarios, they do so towards the areas in the east of the study region. This agrees to the expected trends in the increase in annual mean temperature, annual

precipitation and annual precipitation in the warmest quarter of the studied area. For amphibians, these variables are key to their life requirements associated with the reproduction and development of embryos and larvae (Walls et al., 2013). But also, these climate changes could affect indirectly by altering the availability of prey, and the dynamics of pathogens and stressors. These complex interactions could lead to the populations decline (Blaustein et al., 2010). These changes in different bioclimatic variables were synthesized in the modelled trends of the humid subtropical region projected for 2100 under different intensities of GHG emissions (Rubel & Kotteck, 2010). On the basis of mid-range climate-warming scenarios, some authors predicted that 15–37% of the species will go extinct by 2050, including 13–68% of amphibians (Thomas et al., 2004). Several authors have predicted changes in the distribution, abundance and life cycle of amphibians as a consequence of climate change for different parts of the world (Araújo et al., 2006; Hilbert et al., 2007; Toranza, 2011). In addition, they suggested that the displacements of the isotherms produce a warming of the colder regions, which favours the appearance of areas that are likely to be colonized such as it was observed in richness pattern of our study.

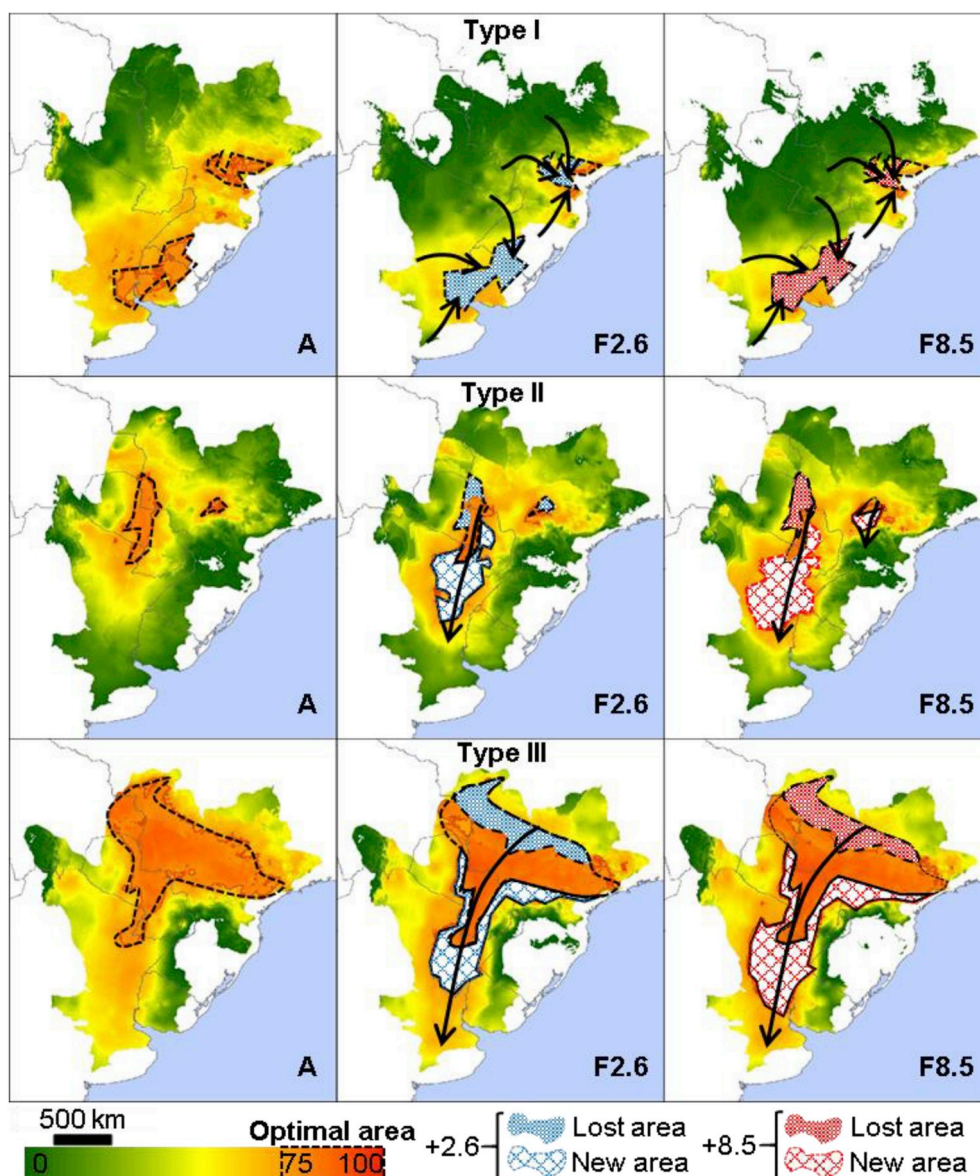


Fig. 4. Examples of different shift-type pattern of potential distribution maps obtained with MaxEnt under (A) current climatic conditions averaged over the period 1950–2000 (WorldClim v1.4); and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W/m}^2$ (F2.6) and $+8.5 \text{ W/m}^2$ (F8.5). The three patterns are exemplified with the changes in distribution ranges of *Leptodactylus gracilis*, *Scinax acuminatus* and *Rhinella bergi* for Types I, II and III, respectively. Dotted lines delimit the optimal distribution areas and the arrows the direction in which the range is displaced.

Table 5

Average overlap between distributions for future scenarios 26_50 and 85_50 and the current distribution for each ecological group (SE: standard error).

Ecological group	Species	Overlap 26_50	Overlap 85_50
		Mean (+/- SE)	Mean (+/- SE)
1	10	26.7 (6.7)	31.7 (10.1)
2	9	32.4 (7.4)	22.3 (6.6)
3	10	19.1 (6.4)	19.8 (6.6)
4	11	21.9 (6.2)	30.6 (9.4)
5	1	23.0	17.0
6	1	77.0	88.0

In brief, our models predicted that the conditions driven by the two considered future scenarios would be unfavourable for the studied amphibian species due to a reduction or increased fragmentation of the current distribution area, or their combination. They are expected to face complex conservation issues, highlighting the need to propose urgent

measures aimed at mitigating climate change in the region, such as protection of key areas and maintenance and control of quality of shallow water-bodies. From a strategic point of view, the knowledge of which are the overlapping areas between current and potential future distributions allows to identify priority areas for species conservation by preventing habitat loss due to different types of land use (Blaustein & Wake, 1990). Likewise, shallow-water monitoring in the priority areas could be a useful tool to avoid the contamination of mating and breeding sites, which has been reported to be a major mortality factor (Gardner, 2001).

Finally, changes in the distribution area of the studied amphibian species will probably be more complex than depicted above due to the rapid land-use and land-cover changes taking place in the region over the last decades (and that will probably continue for the next years). Indeed, large wetland areas are affected by expansion of the agricultural frontier, livestock intensification, urban growth and water infrastructure and management (Benzaquén, 2013; Davidson, 2014; Junk, 2013; Paruelo et al., 2006; Sica, Quintana, Radeloff, & Gaviera-Pizarro, 2016). As a result, the Paraná Basin, the main basin in the

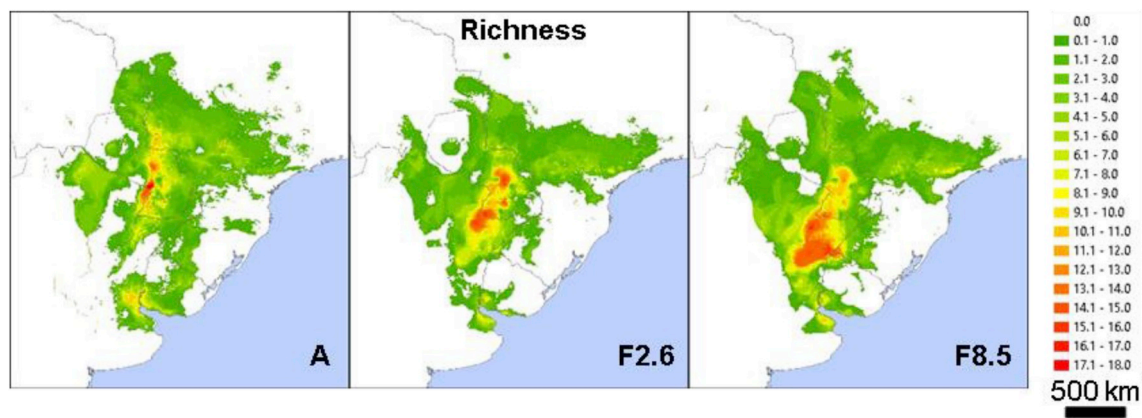


Fig. 5. Potential richness of the considered amphibians species modelled by MaxEnt under (A) current climatic conditions and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W/m}^2$ (F2.6) and $+8.5 \text{ W/m}^2$ (F8.5). The colour code on the right side represents potential richness from lower (green) to higher (red) number of species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

study area, currently supports the largest number of threatened species of mammals, birds, amphibians and crocodiles worldwide (International Rivers, 2015). In this context, it is most likely that the situations predicted for the studied species may also apply to other wetlands species of the region.

5. Conservation implications

Distribution models are useful tools that contribute to the development of plans, strategies and public policies regarding biodiversity management and conservation, by predicting the impacts of climate change on species distributions under different future scenarios (Biringier et al., 2005; Cayuela et al., 2009; Mawdsley, O'Malley, & Ojima, 2009). In our study, we focused on amphibians because of their key role in the trophic dynamics of ecosystems either as prey or predator roles (Gardner, 2001), in the biological control of arthropod pest populations, and in maintaining energy and carbon fluxes (Guyer & Gentry, 1990; Pearman, 1997). In addition, they have complex life cycles in which different developmental stages occupy different habitats, usually aquatic and terrestrial, and feed on different food resources (Whiles et al., 2006). At present, amphibians are suffering from numerous pressures mentioned above which have caused the greatest declines. This leads to an increase in the risk of extinction, which is enhanced by the effects of climate change (Hocking & Babbitt, 2014).

Habitat loss and fragmentation are known to be major threats for biodiversity conservation (Opdam & Wascher, 2004; Santos & Tellería, 2006). At biogeographical scale, habitat loss can be detected by a reduction in the optimal species area, while fragmentation is noticed as an increase in the number of suitable patches. The combined action of both processes result in the isolation of populations, thus increasing the

probability of species extinction at local and possibly regional scale (Corn & Fogleman, 1984). In fact, these processes are recognised as the major factors contributing to the decline of many amphibian populations (GAA, 2006). In the context of potential future distribution, our results indicate that 2 species (5%) will suffer from habitat loss and fragmentation under both climate forcing scenarios (*Phyllomedusa sauvagii* and *Trachycephalus typhonius*). Although these species are not currently threatened, they would be in the near future according with the observed changes. Furthermore, *Trachycephalus typhonius*, *Leptodactylus bufonius* and *L. gracilis* were the species most affected by climate projections since they lost their current distribution areas, and the new ones had a less total area without overlap of patches.

Otherwise *Lepidobatrachus asper*, classified as near threatened (IUCN, 2015), could be benefited due to the future conditions and, in this way, improve its conservation status. However, it is necessary to consider local factors (e.g., land use change) that could affect it due to its particular adaptations to xerophytic forests. Besides, Cayuela et al. (2009) warns that species distribution models shows lower predictive ability for high-conservation value species (e.g., rarest or most threatened species) due to the scarce data records. This is in agreement with our study, where the occurrence records of seven species (including the two endangered species *Argenteohyla siemersi* and *Melanophryniscus devincenzii*; IUCN, 2015) were insufficient to model its geographical distribution (Appendix C).

Due to the amphibians low dispersion capacity (Smith & Green, 2005) the overlap of present and future scenarios distributions modelled allow decision makers to identify priority areas for conservation for this species in LPB. The earlier detection of such future situation could allow for the implementation of measures in order to decrease potential risks to which the species could be subject.

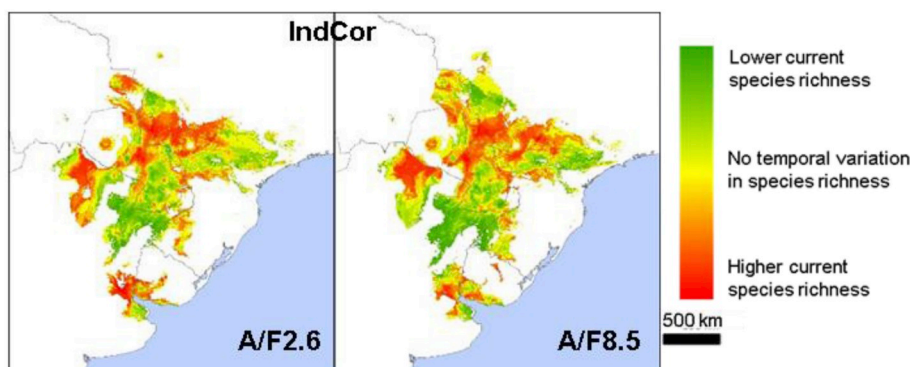


Fig. 6. Map of the study area generated with the IndCoR index calculated as current species richness (A) over species richness for projected future scenarios (F2.6: $+2.6 \text{ W/m}^2$, and F8.5: $+8.5 \text{ W/m}^2$). The colour code on the right side represents IndCoR values from lower (red) to higher (dark green) current species richness. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Author contributions

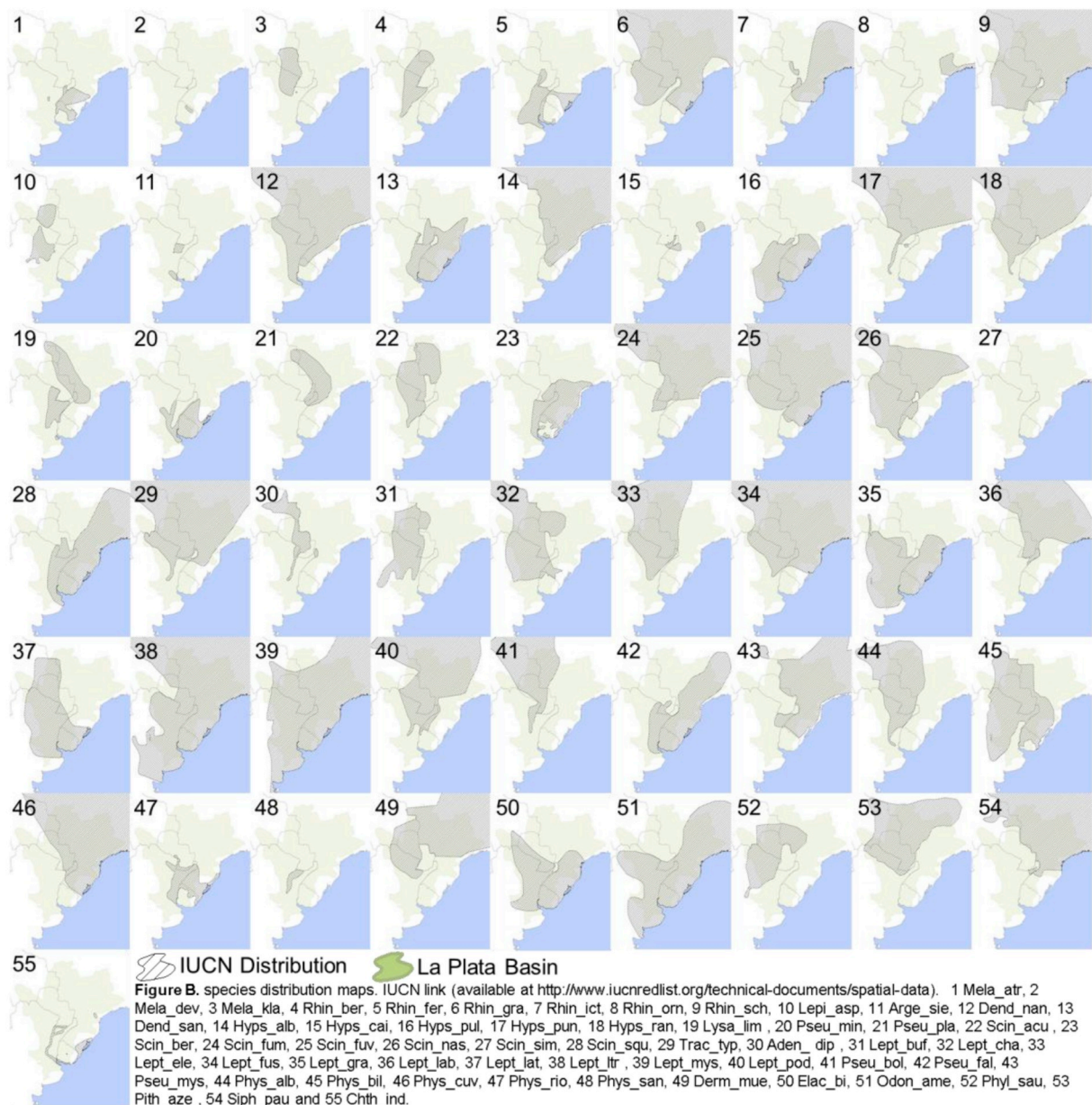
FS and RQ conceived the ideas; FS performed the bioclimatic modelling and species distribution; VB made the maps and the spatial analyses of the species distributions; PK performed the statistical calculations. All authors contributed to the drafting of the manuscript, and gave final approval for publication.

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Appendix A. Species distribution. The IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>



Appendix B. Ecological traits. Reproductive period: Spring-Summer (SS), Annual (A), Autumn-Winter (AW). **Reproductive patterns:** Explosive (E): species with breeding activity lasting one or a few days (Wells, 1977), Continuous (C): species with individuals reproducing throughout the year (sensu Crump, 1974), Prolonged (P): species reproducing for more than three consecutive months (sensu Wells, 1977). **Habitat use for breeding:** Temporary Waterbodies (TW), Temporary Waterbodies After Rain (TWAR), Permanent Waterbodies (PW), Over Vegetation (V), Hole (H). **Habitat preferences:** Grassland (G), Rainforest (RF), Xerophytic Forest (XF), Wetlands (W). nd: No data

Family	Species	Acronym	Reproductive period	Reproductive patterns	Habitat use for breeding	Habitat preferences	Ecological group
Bufonidae	<i>Rhinella bergi</i>	<i>Rhin_ber</i>	SS	nd	TW	G	1
Bufonidae	<i>Rhinella icterica</i>	<i>Rhin_ict</i>	nd	nd	TW	G	1
Hylidae	<i>Pseudis minuta</i>	<i>Pseu_min</i>	nd	nd	PW	W	1
Hylidae	<i>Scinax fuscovarius</i>	<i>Scin_fuv</i>	SS	nd	TWAR	G	1
Hylidae	<i>Scinax similis</i>	<i>Scin_sim</i>	nd	nd	V	W	1
Leptodactylidae	<i>Leptodactylus bufoninus</i>	<i>Lept_buf</i>	SS	nd	PW	G	1
Leptodactylidae	<i>Leptodactylus labyrinthicus</i>	<i>Lept_lab</i>	nd	nd	TW	G	1
Leuperidae	<i>Physalaemus cuvieri</i>	<i>Phys_cuv</i>	nd	nd	TW	G	1
Microhylidae	<i>Dermatonotus muelleri</i>	<i>Derm_mue</i>	nd	nd	TW	XF	1
Typhlonectidae	<i>Chthonerpeton indistinctum</i>	<i>Chth_ind</i>	SS	nd	H	G	1
Hylidae	<i>Scinax acuminatus</i>	<i>Scin_acu</i>	A	E	V	G	2
Hylidae	<i>Scinax nasicus</i>	<i>Scin_nas</i>	A	P	V	G	2
Hylidae	<i>Scinax squalirostris</i>	<i>Scin_squ</i>	A	C	V	G	2
Leptodactylidae	<i>Leptodactylus podicipinus</i>	<i>Lept_pod</i>	A	P	TW	G	2
Leptodactylidae	<i>Pseudopaludicola mystacalis</i>	<i>Pseu_mys</i>	A	nd	V	G	2
Leuperidae	<i>Physalaemus biligonigerus</i>	<i>Phys_bil</i>	A	P	TW	G	2
Odontophrynidae	<i>Odontophrynus americanus</i>	<i>Odon_ame</i>	A	P	TWAR	G	2
Phyllomedusidae	<i>Phyllomedusa sauvagii</i>	<i>Phyl_sau</i>	A	E	V	XF	2
Phyllomedusidae	<i>Pithecopus azureus</i>	<i>Phyl_azu</i>	A	C	V	XF	2
Hylidae	<i>Dendropsophus nanus</i>	<i>Dend_nan</i>	A	C	PW	G	3
Hylidae	<i>Dendropsophus sanborni</i>	<i>Dend_san</i>	A	C	PW	G	3
Hylidae	<i>Hypsiboas albopunctatus</i>	<i>Hyps_alb</i>	SS	C	PW	W	3
Hylidae	<i>Hypsiboas raniceps</i>	<i>Hyps_ran</i>	SS	C	TW	W	3
Hylidae	<i>Scinax berthae</i>	<i>Scin_ber</i>	SS	C	TW	W	3
Hylidae	<i>Scinax fuscomarginatus</i>	<i>Scin_fum</i>	SS	C	V	W	3
Leptodactylidae	<i>Leptodactylus elenae</i>	<i>Lept_ele</i>	SS	C	TW	G	3
Leptodactylidae	<i>Leptodactylus gracilis</i>	<i>Lept_gra</i>	SS	C	H	G	3
Leptodactylidae	<i>Leptodactylus latinasus</i>	<i>Lept_lat</i>	SS	C	PW	G	3
Leptodactylidae	<i>Leptodactylus mystacinus</i>	<i>Lept_mys</i>	SS	C	H	G	3
Bufonidae	<i>Rhinella fernandezae</i>	<i>Rhin_fer</i>	SS	E	TWAR	RF	4
Bufonidae	<i>Rhinella granulosa</i>	<i>Rhin_gra</i>	A	E	TW	G	4
Bufonidae	<i>Rhinella schneideri</i>	<i>Rhin_sch</i>	SS	E	TWAR	G	4
Hylidae	<i>Lysapsus limellum</i>	<i>Pseu_lim</i>	A	C	TW	W	4
Hylidae	<i>Trachycephalus typhonius</i>	<i>Trac_yen</i>	A	E	TW	G	4
Leptodactylidae	<i>Leptodactylus chaquensis</i>	<i>Lept_cha</i>	SS	E	TW	G	4
Leptodactylidae	<i>Leptodactylus latrans</i>	<i>Lept_oce</i>	A	E	TW	W	4
Leptodactylidae	<i>Pseudopaludicola falcipes</i>	<i>Pseu_fal</i>	A	E	TW	W	4
Leuperidae	<i>Physalaemus riograndensis</i>	<i>Phys_rio</i>	SS	E	TW	G	4
Leuperidae	<i>Physalaemus santafecinus</i>	<i>Phys_san</i>	A	E	TWAR	G	4
Microhylidae	<i>Elachistocleis bicolor</i>	<i>Elac_bi</i>	SS	E	TWAR	G	4
Hylidae	<i>Hypsiboas pulchellus</i>	<i>Hyps_pul</i>	AW	P	V	RF	5
Ceratophryidae	<i>Lepidobatrachus asper</i>	<i>Lept_asp</i>	nd	E	TWAR	XF	6

Appendix C. Species occurrence dataset. Georeferenced records of amphibian species used for distribution modelling and AUC values obtained for each species with MaxEnt, BIOCLIM and DOMAIN algorithms. G.R. georeferenced records

Acronym	G.R.	Algorithm AUC		
		MaxEnt	Bioclim	Domain
<i>Mela_atr</i>	2 ^a			
<i>Mela_dev</i>	1 ^a			
<i>Mela_kla</i>	2 ^a			
<i>Rhin_ber</i>	14	0.974	0.532	0.933
<i>Rhin_fer</i>	81	0.994	0.724	0.873
<i>Rhin_gra</i>	388	0.961	0.700	0.920
<i>Rhin_ict</i>	46	0.994	0.671	0.969
<i>Rhin_orn</i>	1 ^a			
<i>Rhin_sch</i>	207	0.975	0.636	0.824
<i>Lepi_asp</i>	13	0.985	0.712	0.913
<i>Arge_sie</i>	4 ^a			
<i>Dend_nan</i>	243	0.982	0.702	0.806
<i>Dend_san</i>	52	0.994	0.675	0.913
<i>Hyps_alb</i>	61	0.984	0.724	0.890
<i>Hyps_cai</i>	6 ^b	0.944	0.770	0.940
<i>Hyps_pul</i>	205	0.984	0.746	0.864
<i>Hyps_pun</i>	160	0.975	0.797	0.882

<i>Hyps_ran</i>	201	0.981	0.726	0.828
<i>Lysa_lim</i>	105	0.986	0.679	0.909
<i>Pseu_min</i>	50	0.993	0.829	0.972
<i>Pseu_pla</i>	2 ^a			
<i>Scin_acu</i>	102	0.984	0.738	0.903
<i>Scin_ber</i>	27	0.997	0.675	0.888
<i>Scin_fum</i>	60	0.989	0.634	0.929
<i>Scin_fuv</i>	138	0.984	0.691	0.858
<i>Scin_nas</i>	171	0.981	0.675	0.817
<i>Scin_sim</i>	6 ^b	0.957	0.670	0.870
<i>Scin_squ</i>	48	0.993	0.622	0.857
<i>Trac_typ</i>	518	0.953	0.654	0.819
<i>Aden_dip</i>	3 ^a			
<i>Lept_buf</i>	109	0.985	0.716	0.876
<i>Lept_cha</i>	211	0.982	0.738	0.830
<i>Lept_ele</i>	62	0.994	0.763	0.912
<i>Lept_fus</i>	379	0.963	0.651	0.806
<i>Lept_gra</i>	86	0.984	0.605	0.877
<i>Lept_lab</i>	37	0.981	0.508	0.907
<i>Lept_lat</i>	133	0.987	0.760	0.907
<i>Lept_ltr</i>	422	0.958	0.575	0.758
<i>Lept_mys</i>	283	0.959	0.418	0.834
<i>Lept_pod</i>	185	0.981	0.650	0.850
<i>Pseu_bol</i>	37	0.990	0.815	0.944
<i>Pseu_fal</i>	105	0.987	0.702	0.873
<i>Pseu_mys</i>	37	0.993	0.734	0.971
<i>Phys_alb</i>	99	0.992	0.729	0.907
<i>Phys_bil</i>	117	0.986	0.669	0.917
<i>Phys_cuv</i>	113	0.977	0.729	0.903
<i>Phys_rio</i>	11 ^b	0.917	0.630	0.890
<i>Phys_san</i>	13 ^b	0.868	0.650	0.910
<i>Derm_mue</i>	42	0.984	0.678	0.851
<i>Elac_bi</i>	59	0.987	0.606	0.837
<i>Odon_ame</i>	178	0.980	0.712	0.837
<i>Phyl_sau</i>	49	0.991	0.729	0.905
<i>Pith_aze</i>	54	0.992	0.674	0.878
<i>Siph_pau</i>	7 ^b	0.898	0.550	0.979
<i>Chth_ind</i>	15	0.996	0.826	0.982

^a Insufficient data to model.

^b Few records to obtain models of spatial distribution with areas of high probability of occurrence.

Appendix D. Percentage contribution of each bioclimatic variable to the distribution model of each amphibian species

Acronym	BIO01	BIO02	BIO05	BIO12	BIO14	BIO18	Ecological group
<i>Rhin_ber</i>	46.0	0.6	0.6	8.7	17.7	26.4	1
<i>Rhin_fer</i>	16.6	15.0	0.2	27.4	31.9	8.8	4
<i>Rhin_gra</i>	27.2	0.7	1.5	39.2	9.9	21.5	4
<i>Rhin_ict</i>	15.6	6.2	0.8	13.2	21.9	42.3	1
<i>Rhin_sch</i>	26.3	14.2	1.4	6.6	5.3	46.1	4
<i>Lepi_asp</i>	45.7	1.4	0.3	22.2	3.4	27.1	6
<i>Dend_nan</i>	15.3	12.2	0.5	19.0	14.3	38.7	3
<i>Dend_san</i>	23.7	8.9	0.1	25.1	33.6	8.5	3
<i>Hyps_alb</i>	6.4	14.8	0.3	44.0	2.0	32.6	3
<i>Hyps_pul</i>	47.9	3.8	3.7	3.9	7.4	33.3	5
<i>Hyps_ran</i>	24.3	7.4	2.2	22.9	11.5	31.7	3
<i>Lysa_lim</i>	17.4	6.8	3.1	37.9	32.1	2.7	4
<i>Pseu_min</i>	33.0	1.0	3.2	8.4	53.2	1.2	1
<i>Scin_acu</i>	27.2	6.6	3.7	11.8	12.3	38.4	2
<i>Scin_ber</i>	28.9	6.0	0.4	1.6	62.9	0.2	3
<i>Scin_fum</i>	9.7	8.3	0.6	35.3	12.2	33.9	3
<i>Scin_fuv</i>	17.2	13.7	0.5	3.7	6.0	59.0	1
<i>Scin_nas</i>	26.0	9.3	1.2	16.2	7.7	39.6	2
<i>Scin_sim</i>	59.7	8.0	0.1	6.0	1.2	25.1	1
<i>Scin_squ</i>	29.1	6.5	0.8	25.8	37.3	0.5	2
<i>Trac_typ</i>	31.4	1.4	3.2	41.8	4.0	18.1	4
<i>Lept_buf</i>	27.1	16.5	3.8	8.9	6.5	37.2	1
<i>Lept_cha</i>	24.1	13.8	1.7	8.8	5.0	46.6	4
<i>Lept_ele</i>	22.4	12.9	3.2	5.6	11.8	44	3
<i>Lept_gra</i>	32.3	4.8	1.3	3.0	11.5	47.1	3
<i>Lept_lab</i>	22.8	3.1	0.7	46.8	8.6	18.0	1
<i>Lept_lat</i>	39.9	4.3	0.9	7.0	2.6	45.3	3
<i>Lept_ltr</i>	38.1	2.0	1.7	34.3	9.6	14.2	4
<i>Lept_mys</i>	30.3	5.3	0.6	15.6	7.1	41.2	3
<i>Lept_pod</i>	16.9	11.7	1.8	18.3	11.8	39.6	2
<i>Pseu_fal</i>	16.4	8.6	0.7	43.1	20.2	10.9	4
<i>Pseu_mys</i>	16.7	9.0	0.8	33.1	4.2	36.2	2
<i>Phys_alb</i>	25.9	11.2	2.6	8.7	8.9	42.7	2

<i>Phys_bil</i>	24.6	14.1	0.9	7.4	4.6	48.5	1
<i>Phys_cuv</i>	12.2	6.8	0.4	60.4	5.6	14.7	4
<i>Phys_san</i>	85.9	0.0	0.0	0.1	3.9	10.1	4
<i>Derm_mue</i>	35.4	3.1	2.1	15.7	9.3	34.5	1
<i>Elac_bi</i>	17.2	12.3	1.8	7.9	25.5	35.4	4
<i>Odon_ame</i>	42.3	8.2	2.4	6.4	18.5	22.2	2
<i>Phyl_sau</i>	23.4	11.4	2.4	11.8	10.5	40.6	2
<i>Pith_aze</i>	31.8	9.8	5.7	13.1	9.7	29.9	2
<i>Chth_ind</i>	28.4	2.3	1.0	40.1	27.8	0.4	1

Appendix E. Species distribution models

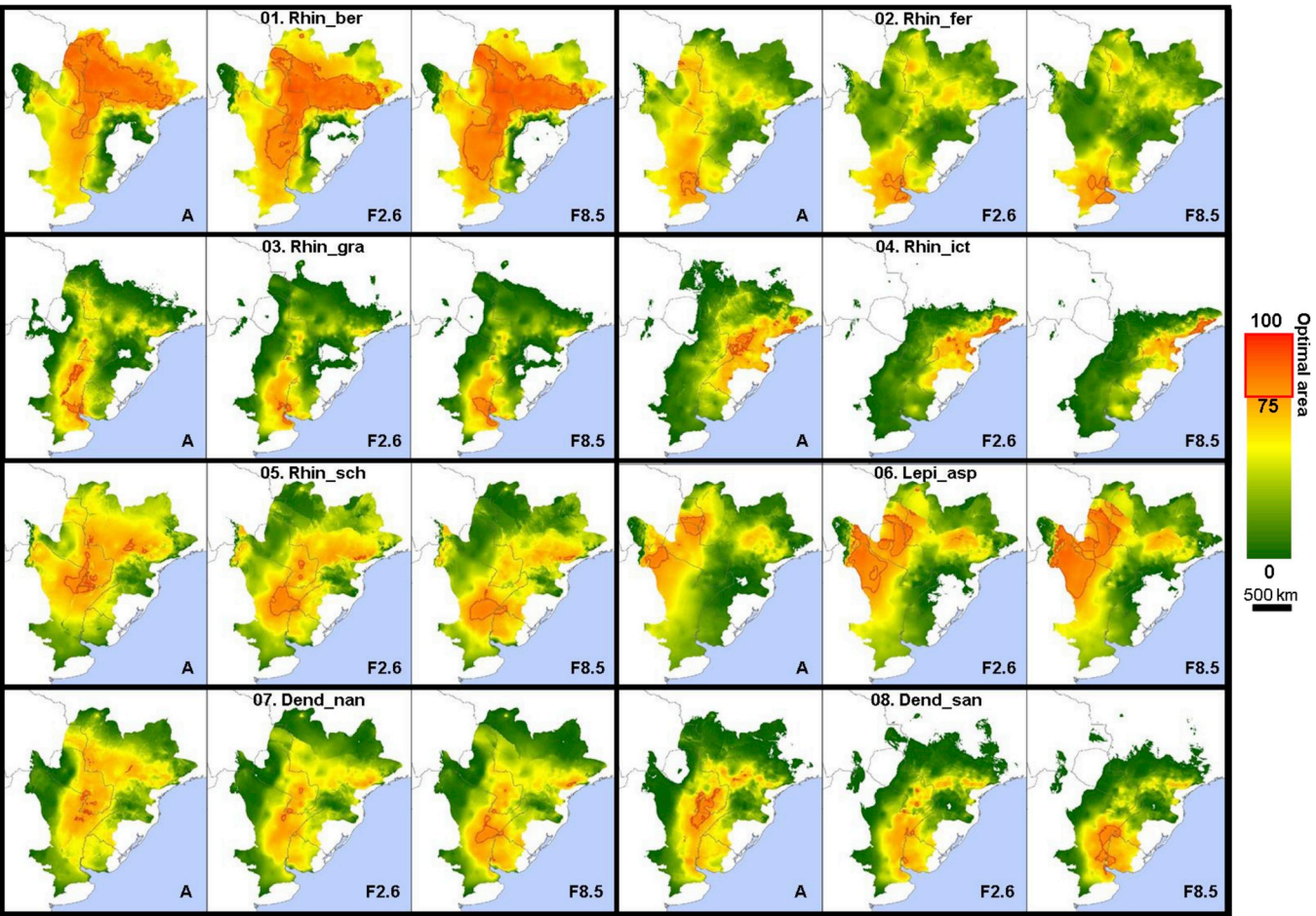


Fig. E. 01 – C. 08. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of +2.6 W / m2 (F1) and +8.5 W / m2 (F2). For acronyms of species names see [Appendix B](#).

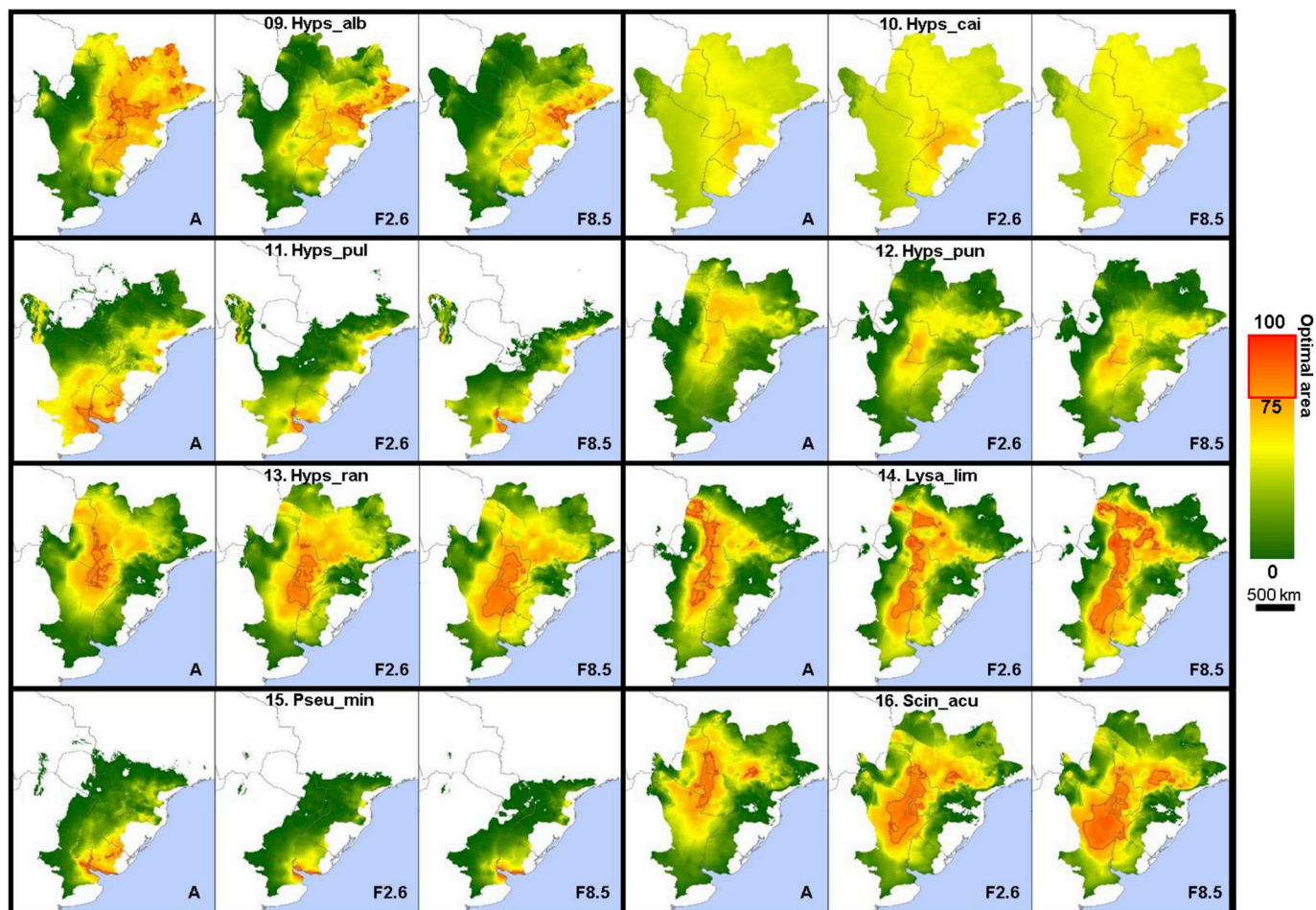


Fig. E. 09 – C. 16. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W} / \text{m}^2$ (F1) and $+8.5 \text{ W} / \text{m}^2$ (F2). For acronyms of species names see [Appendix B](#).

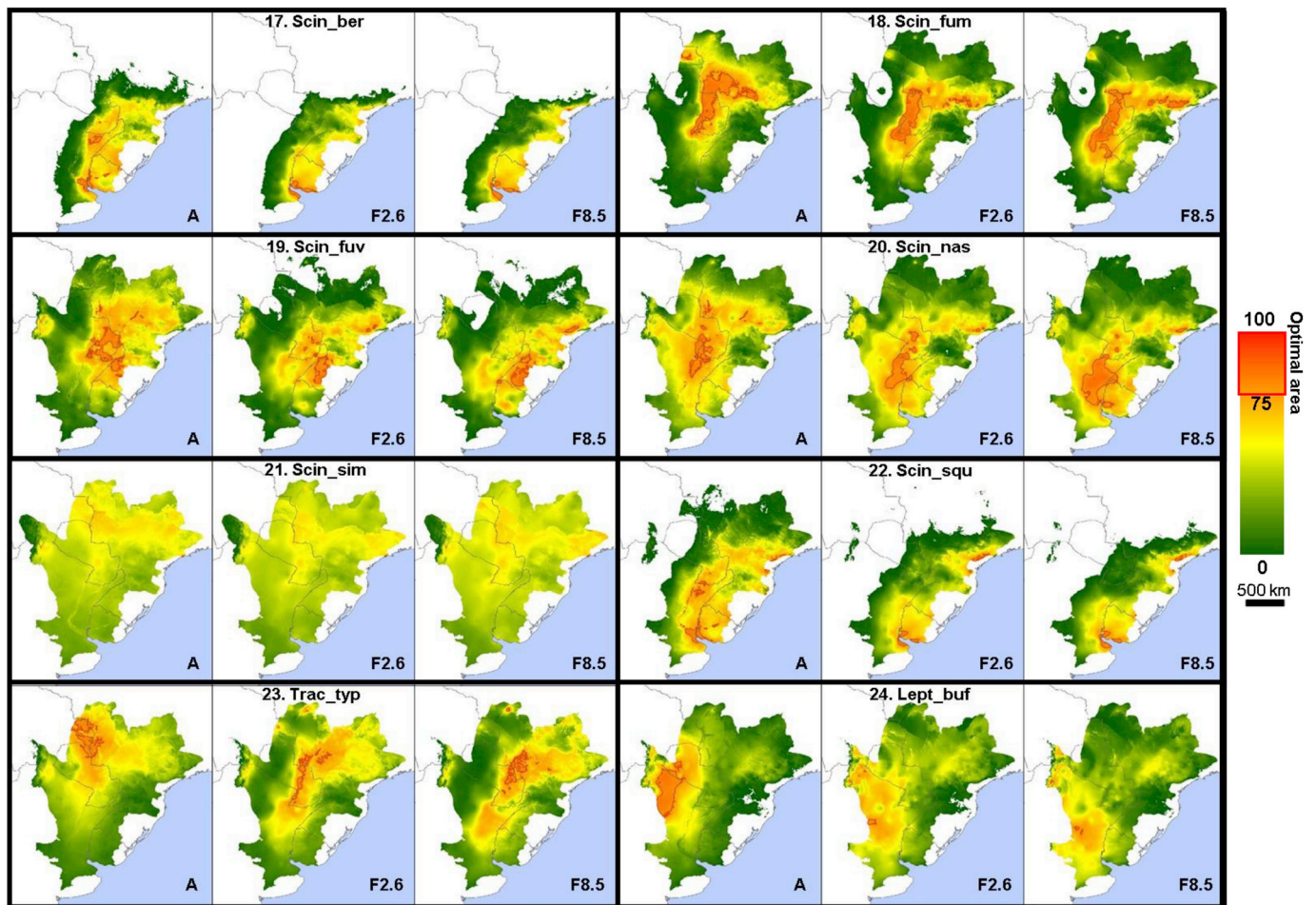


Fig. E. 17 – C. 24. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W} / \text{m}^2$ (F1) and $+8.5 \text{ W} / \text{m}^2$ (F2). For acronyms of species names see [Appendix B](#).

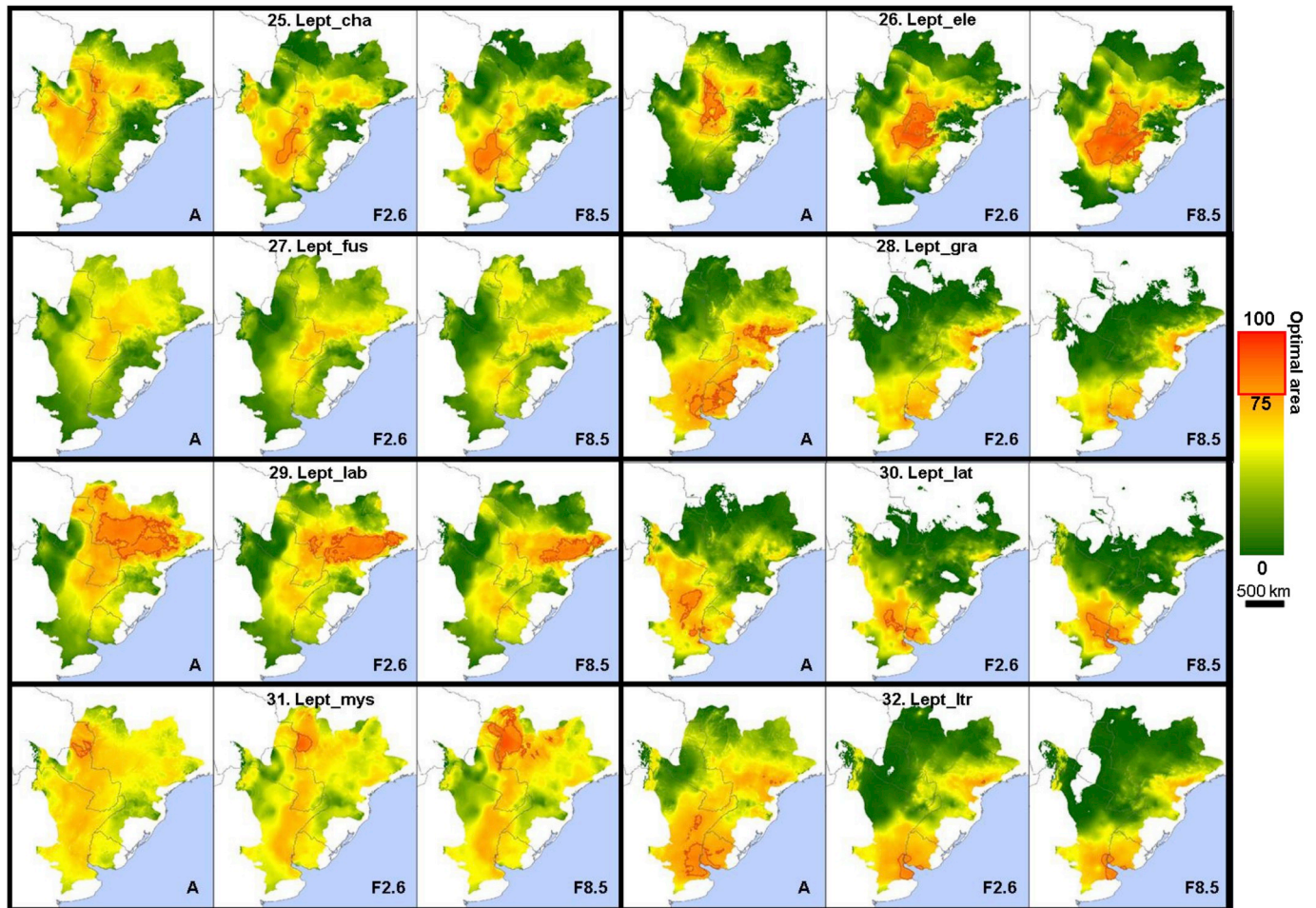


Fig. E. 25 – C. 32. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W} / \text{m}^2$ (F1) and $+8.5 \text{ W} / \text{m}^2$ (F2). For acronyms of species names see [Appendix B](#).

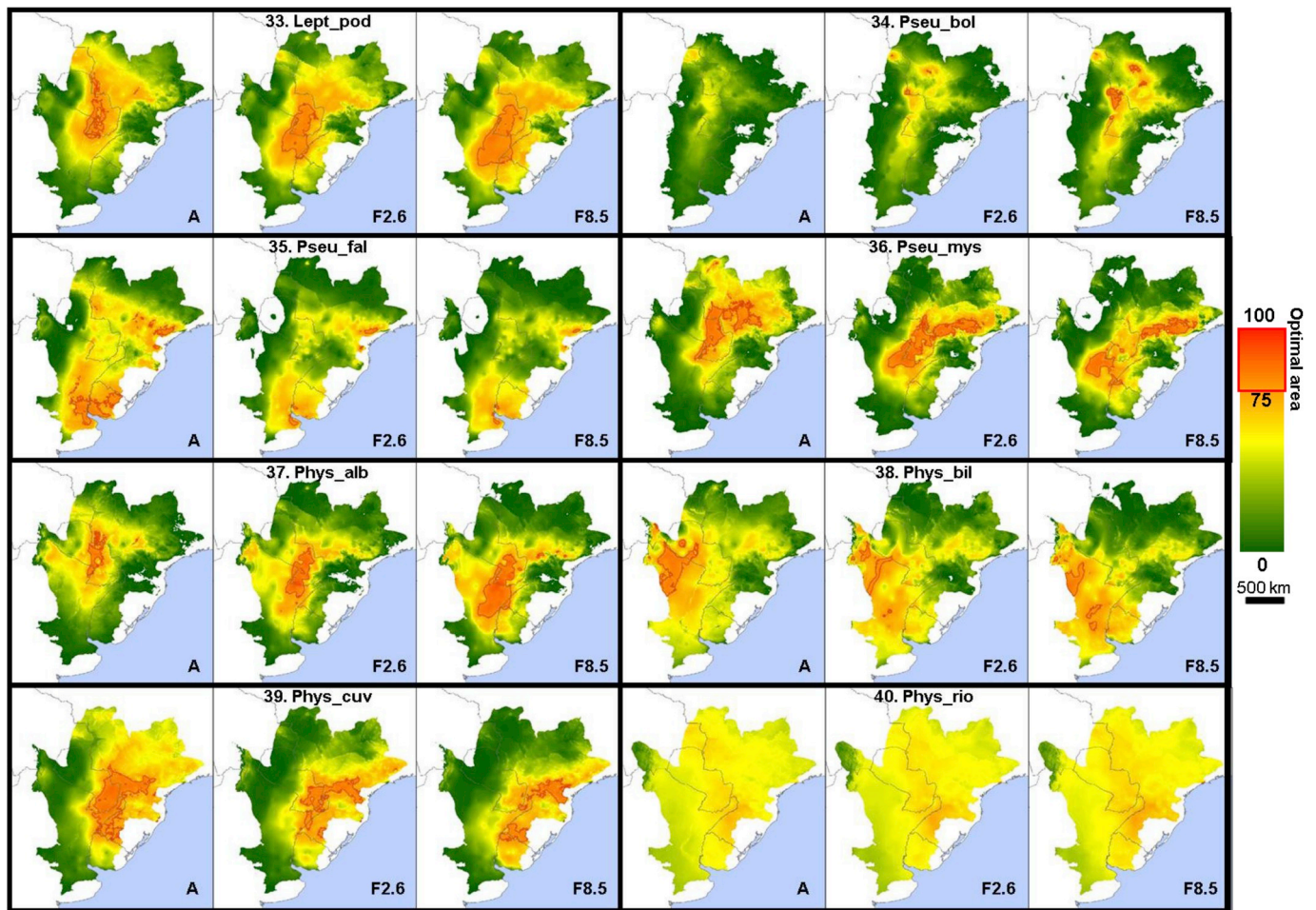


Fig. E. 33 – C. 40. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W / m}^2$ (F1) and $+8.5 \text{ W / m}^2$ (F2). For acronyms of species names see [Appendix B](#).

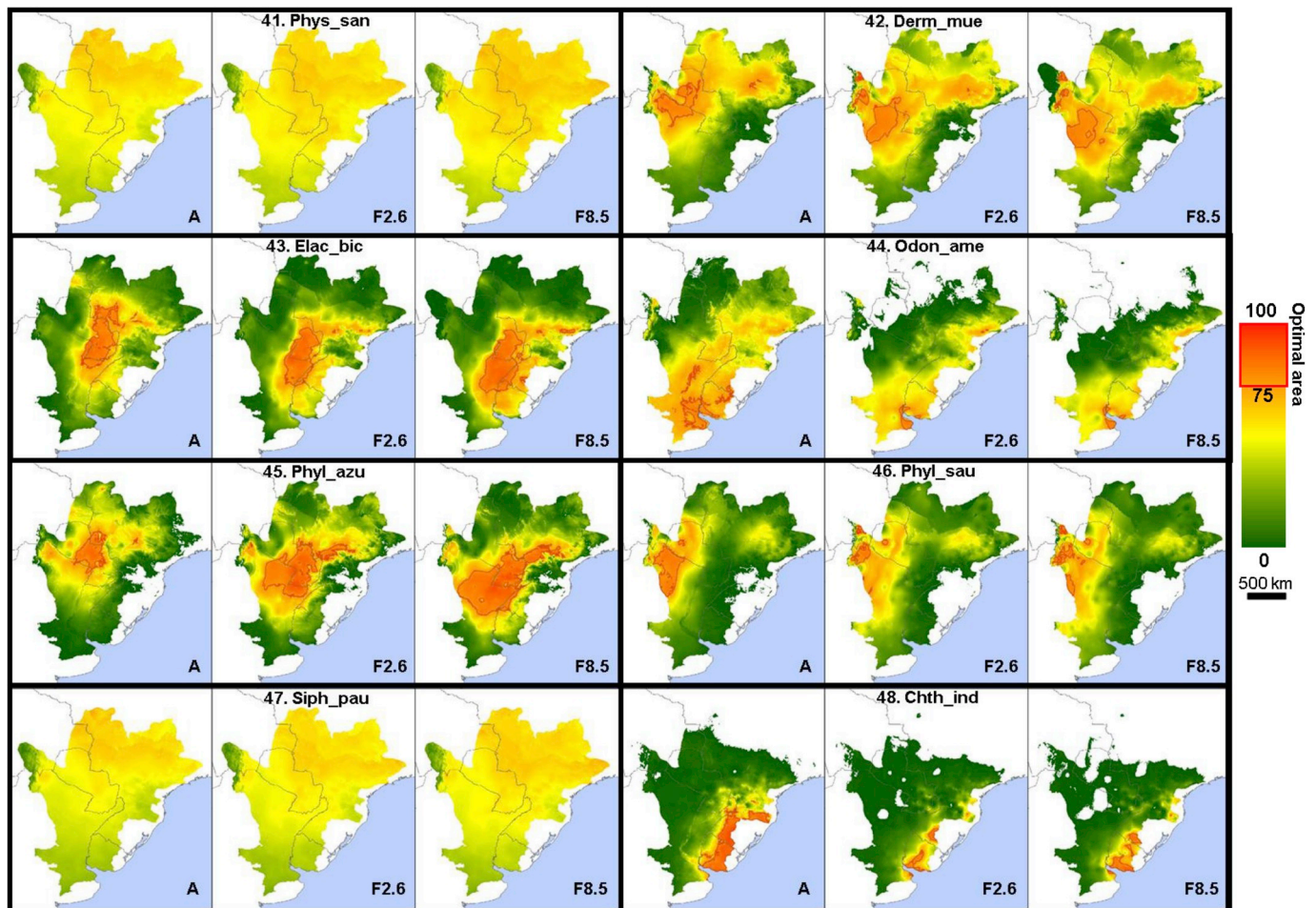


Fig. E. 41 – C. 48. Map of potential distribution generated by MaxEnt for: A-current climatic conditions averaged over the period 1960–1990 (WorldClim v1.3) and potential scenarios to 2050 obtained by the HadGEM2-ES model for GHG climate forcing at concentrations of $+2.6 \text{ W/m}^2$ (F1) and $+8.5 \text{ W/m}^2$ (F2). For acronyms of species names see [Appendix B](#).

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